

CONSIDERATIONS ON THE EVOLUTION OF LICHENS

Harold Robinson
Department of Botany
Smithsonian Institution, Washington, D.C. 20560.

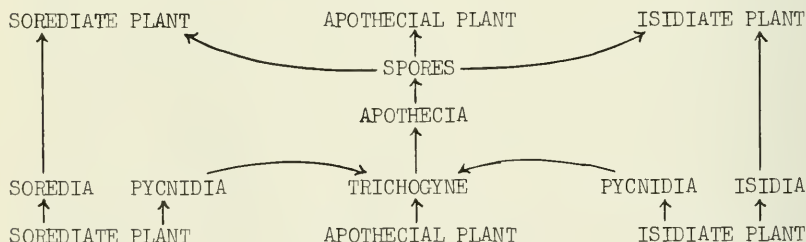
To the casual observer the taxonomic study of lichens does not seem much different from that of other groups of plants. The process of cataloguing phenotypes has produced listings of families, genera, and species. The variations and functions of lichen structures have been studied. Ecological tolerances have been recorded. Phytogeographical data have been plotted. Chemical characters have been used extensively. There is one difference in lichen taxonomy, however, that affects the interpretation of all the other aspects. In lichenology there is no direct knowledge of progeny or genetics. Concepts of populations are reconstructed entirely from examination of static characters of individual specimens with no proof that "species" reliably reproduce their own kind. Until recently not a single lichen had been carried through to a second generation experimentally.

For the valid work of cataloguing phenotypes there is no need to know precise relationships, but recently lichenologists have begun to speculate on the origins of some species. Most important of these is the suggestion by Poelt (1972) that some sorediate and isidiate species would always be the derivatives of non-sorediate and non-isidiate apothecial forms and they could never be ancestral to such forms. Such a concept is the ultimate result of the belief that every phenotype in lichens is the monophyletic result of oneway mutations. Unsaid but implied by such a concept is the presence of unseen tendencies among the vast majority of lichens to produce these recurring mutations. One would suspect that there is an easier explanation for the manner that sorediate, isidiate, and chemical characters recur in so many different combinations in lichens.

An answer to the recurring characters of lichens might be found in sexual reproduction and hybridization. Lichens do possess structures for a sexual life cycle. The question remains, why do lichens have sexual reproduction and how much does it function? Part of the answer is found in the same basic reasons why any organism has sexual reproduction: sex allows favorable mutations to come together in one individual and allows elimination of unfavorable mutations. The non-sexual organism is barred from gaining any favor-

able mutation, even one in a close relative, or rejecting deleterious genes, except by separate and rare mutations. Animals, plants and even bacteria have all developed ways of trading genetic material and they have maintained these systems with very few exceptions. Sexual reproduction and recombination of genes has played a major role in evolution of other groups, and it seems likely that it has done the same in lichens.

The theoretical life-cycle of the lichen is well known. The various structures such as pycnidia, spermatia, trichogynes, ascogenous hyphae and asci are in all mycological texts. The apothecia and perithecia of lichens are the most obvious aspects of the life-cycle but the most functionally important are the pycnidia and trichogynes. Sorediate and isidiate lichens that lack apothecia may have pycnidia. What would happen if the spermatia from a sorediate lichen managed to reach the trichogyne of an apothecial specimen? Would plants that differ only by sorediate or isidiate conditions or by a few chemicals or by ecological tolerances (Gulberson, 1969) be unable to fertilize each other? The biological barriers to fertilization need not be closely correlated with other characters.



It is true that sorediate, isidiate, and apothecial lichens are all capable of perpetuating themselves indefinitely without interbreeding with each other, and perhaps, for the most part, they do. It might be difficult for spermatia of one lichen to reach the trichogyne of another lichen even when the two were entangled on the same twig. Still, if it happened only once in a million years it would provide a simple explanation for the recurring combinations of lichen characters.

There is no reason why hybrids in lichens would produce any strange or unknown combinations of characters. The plants studied by lichenologists are all

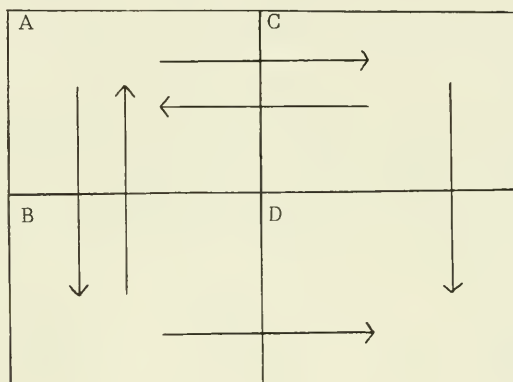
supposedly haploid. The only truly hybrid cells in the lichen are in the ascogenous hyphae and the spores already have the reseggregated genes of the next generation. If single gene differences were involved or two genes that were closely linked then the spores would give rise to plants exactly like the two parents. If more characters are involved and they are not closely linked on the same chromosome then recombinations of parental genotypes can occur. What is most important to recognize is that two genotypes can come from the same ascus and innumerable "species" might come from the spores of the same apothecial plant without any indication unless their precise origin were traced. The spores could give rise to perfectly recognizable and even ecologically distinct forms.

Culture of lichen spores could furnish proof of the presence of hybridization. An initial study of this type has shown minor variations in progeny of *Cladonia cristatella* Tuck. (Ahmadjian, 1964). Proof might be obtained without culturing if the interbreeding species have an observable spore difference. For the present, however, the best evidence of hybridization in lichens is indirect.

Poelt (1972) bases his concept on the phenomenon of species pairs. Actually, the situation in some lichen groups is far more complex. In some cases lichen species can be presented in an interrelated checkerboard pattern. Each species differs from two others by a single character. Often more characters

Species A	Species C
sorediate	non-sorediate
chem X	chem X
Species B	Species D
sorediate	non-sorediate
chem Y	chem Y

and more species are involved in such interrelationships. Such patterns are common enough in some lichen groups that it has hardly seemed necessary to wait for a specimen to describe some of the species. Such patterns often involve only chemical and no sorediate or isidiate forms. No one seems to have looked fully at the implications of such patterns. Even if one assumes the non-sexual origin of such patterns through mutations the probability of getting all four types is no greater than the probability of getting at least one of the types twice. Given the frequency of such



patterns it is inevitable that some of the species involved are polyphyletic. This is true no matter what the mechanism of origin. The concept of species in lichenology would need reevaluation in any case.

It seems unlikely that individual mutations are the source of the variants in the checkerboard patterns and I suggest that they are the products of hybridization and re-segregation of genes. Complete checkerboard patterns could be interpreted to mean that inter-fertilization was possible in the group of species involved. More important from the viewpoint of true phylogeny would be the groups in which such species clusters did not occur.

One excellent study (Culberson & Culberson, 1973; Culberson, 1973) provides evidence on the character stability in one group of apparently closely related species of lichens. The study of the Parmelia hypotropha - P. perforata group (now Parmotrema hypotrophum (Nyl.) Hale and P. perforatum (Jacq.) Mass.

see Hale, 1974) is complicated by the difference in ecological tolerance that correlates with the difference between chemical species. Still, it is evident that the chemically distinct forms must not have produced any recombinations during the post-glacial period in which they have had their present distributions. There is no such evidence for isolation between sorediate and non-sorediate forms which are sympatric and which could hybridize without producing any new combinations of characters. The study shows the fallacy of previous tendencies to value sorediate differences more than chemical differences. The study is flawed only by the acceptance of the Poelt idea that sorediate species are necessarily derived from chemically identical apothecial species by "the production of soredia and the subsequent suppression of sexuality".

The present view of lichen speciation would still accept mutation as the original source of chemical and structural characters but not as the source of most of the numerous present combinations of these characters. The present view would not require much less stability of lichen "species" in nature than is generally suspected, but it would suggest that when changes do occur they are mostly from hybridization rather than from mutation, and that some "species" may have originated more than once.

One can visualize the evolution of lichens being as in other groups of plants, the gradual differentiation of interbreeding populations containing many genotypes. Such lichen populations would include apothecial, sorediate, and isidiate forms along with many chemical variants. Many seeming parallelisms would be the result of genetic recombination, and actual mutation would play a lesser role. Eventual biological isolation would tend to restrict the chemical variations available in any evolving group since only certain variations would be available within the interbreeding group.

The apothecial, sorediate, and isidiate variations of lichens would be more consistently maintained in the populations than would the chemical variants because of the reproductive requirements involved. Any completely sorediate and isidiate forms would require apothecial forms for their sexual reproduction and for the resulting potential for genetic recombination and accelerated evolution. Of course, there might be cases where sorediate forms have become isolated and are really vegetatively reproducing dead-ends with all possible interbreeding apothecial forms extinct.

Apothecial forms of lichens also have a more basic dependence on sorediate and isidiate forms. It would seem that such forms would be the only source from which spores from the apothecia could obtain the lichen symbiont, Trebouxia. This would seem particularly true of soredia. It would require sorediate forms to be present in all populations. Such sources of soredia need not be related closely to the apothecial form and probably often are not as evidenced by the wide distribution of algal species in lichens (Ahmadjian, 1960). The only requirement would be that the hyphae from the spores would be faster growing or possess some other biological advantage over the hyphae already present in the soredium. One can speculate that the extinction of some particularly vulnerable soredial lichen might result in the extinction of many other species that depend on it as a source of Trebouxia. Almost certainly the long evolutionary history of lichens has produced some careful balances between the populations of apothecial and sorediate forms and undoubtedly the hybridization and recombinations play a major role in maintaining this balance.

Literature Cited

- Ahmadjian, V. 1960. Some new and interesting species of Trebouxia, a genus of lichenized algae. *Amer. Jour. Bot.* 47: 677-683.
- _____. 1964. Further studies on lichenized fungi. *The Bryologist* 67: 87-98.
- Culberson, W. L. 1969. The use of chemistry in the systematics of lichens. *Taxon* 18: 152-166.
- _____. 1973. The Parmelia perforata Group: Niche characteristics of chemical races, speciation by parallel evolution, and a new taxonomy. *The Bryologist* 76: 20-29.
- Culberson, W. L. and C. F. Culberson 1973. Parallel evolution in lichen-forming fungi. *Science* 180: 196-198.
- Hale, M. E. 1974. New combinations in the lichen genus Parmotrema Massalongo. *Phytologia* 28: 334-339.

- Poelt, J. 1972. Die taxonomische Behandlung von Artenpaaren bei den Flechten. Bot. Notis. 125: 77-81.

Acknowledgements

I wish to thank Drs. Mason Hale and Ted Esslinger for reading an earlier version of the manuscript and for making some corrections. I also wish to acknowledge a review by Dr. William Culberson which pointed out the need for some revisions.